

The distribution and abundance of deepwater ciscoes in Canadian waters of Lake Superior

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with 8 figures and 5 tables

Abstract: Deepwater ciscoes have declined precipitously in the Laurentian Great Lakes, and only Lake Superior contains a fauna resembling that of the early 20th century. The discovery of areas of high abundance and the identification of habitat preferences in Lake Superior would provide important information for the basin-wide recovery of these species. This research completed the most comprehensive deepwater cisco survey in the nearshore Canadian waters of Lake Superior to (1) determine and compare the current distribution and relative abundance of ciscoes, (2) compare coregonid abundance and community structure at specific sites to historic data, and (3) assess habitat preferences of Lake Superior ciscoes. Deepwater ciscoes remain the dominant prey fishes in Lake Superior, and all four species—*Coregonus artedii*, *C. hoyi*, *C. kiyi* and *C. zenithicus*—remain widely distributed. In general, embayment areas contain the highest densities of all species except *C. kiyi*, which are found offshore, and there are lower densities in the eastern part of the lake. There have been tremendous changes in the cisco community since the historic surveys, with the formerly dominant *C. zenithicus* being replaced by *C. artedii* and *C. hoyi*. Spatial segregation primarily occurred with depth; *C. kiyi* is most abundant in deep water (>130 m), *C. hoyi* and *C. zenithicus* are most abundant at mid-depths (80–110 m), while *C. artedii* is most abundant at depths of <60 m.

Keywords: Lake Superior, Ciscoes, distribution, abundance, habitat.

Introduction

The continuing loss of cisco diversity in the North American Laurentian Great Lakes since the landmark coregonid surveys of KOELZ (1929) is one of the least discussed, but potentially most important, conservation issues facing Great Lakes fishery managers. Ciscoes are now recognized as being important ecological integrators in deep lakes as a trophic connection between benthic invertebrates and piscine predators, and there is interest in restoring ciscoes in areas where they have been extirpated to help stabilize and recover deepwater food webs (FAVÉ & TURGEON 2008). There were once seven cisco species identified from the Great

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Lakes, but three now are believed to be extinct and the remaining communities are greatly diminished (SMITH 1964, SMITH 1972). Lake Superior has the most intact cisco fauna, with four species remaining: *Coregonus artedii*, considered a shallow water species, and *C. hoyi*, *C. kiyi*, and *C. zenithicus*, which collectively make up the deepwater ciscoes. *C. kiyi* is only extant in Lake Superior; Lake Superior also contains one of only two taxonomically accepted populations of *C. zenithicus* (COSEWIC 2009).

Deepwater ciscoes were once part of a sizeable targeted fishery in Lake Superior, with almost 11 million metric tonnes having been harvested from 1894–1950 (HOFF & TODD 2004, CHIARAPPA 2005). *C. zenithicus* constituted more than 90% of the deepwater ciscoes in lakewide surveys in the 1920s (KOELZ 1929), but the most recent surveys in United States waters have documented a tremendous shift in the deepwater community. *C. zenithicus* appears to have been replaced by *C. hoyi* and *C. kiyi* and make up, on average, <5% of the catch in areas where they remain (HOFF & TODD 2004). The *C. zenithicus* decline has primarily been attributed to commercial over-harvest (LAWRIE 1978), although the introduction of invasive species, habitat degradation and inter-specific competition or predation are suggested as being factors that may be limiting recovery (BRONTE et al. 2010). The large decline in deepwater ciscoes has resulted in the listing of *C. kiyi* as a species of Special Concern and the recommendation that *C. zenithicus* be listed as Threatened under Canadian federal Species-at-Risk legislation. Despite the obvious need for a comprehensive deepwater cisco survey in the Canadian waters of Lake Superior, it has never been completed.

Assessing deepwater cisco populations is challenging due to the spatial overlap and morphological plasticity of these species. The three Lake Superior deepwater cisco species and *C. artedii*, which can also be found at similar depths, share physical characteristics and there is no single diagnostic character that separates these species, although together the combination of body shape, head and eye morphology and gill raker counts allow identification of each species (TODD & SMITH 1980, COSEWIC 2009). SELGEBY & HOFF (1996) presented evidence for differences in inter-specific depth distribution, with most *C. zenithicus* and *C. kiyi* found at depths of 105–145 m, most *C. hoyi* at 65–105 m, and *C. artedii* primarily at <65 m, but there remains considerable overlap in the depths used by the three deepwater forms, and very little else is known about the habitat preferences of these three species.

The discovery of areas of high relative abundance and the identification of habitat preferences in Lake Superior would provide important baseline information for planning the basin-wide recovery of these cisco species. The objectives of this study were to (1) determine and compare the current distribution and relative abundance of cisco species across the Canadian waters of Lake Superior, (2) compare coregonid abundance and community structure at specific sites to the analogous historic data from the KOELZ (1929) assessment, and (3) assess habitat (slope, temperature, substrate, and depth) preferences of Lake Superior ciscoes.

Materials and methods

A total of 140 nets were set in the Canadian waters of Lake Superior during four years: 2004, 2006, 2007, and 2008 (Fig. 1). Two types of nets were used in the sampling: a 'traditional' net and an 'experimental' net. The traditional net was composed of four 92 m nylon mesh panels, alternating 64 mm and 70 mm stretch mesh (for a total gang length of 366 m); mesh size and material for the traditional nets were chosen to as closely replicate the nets used in the historic KOELZ (1929) surveys, though KOELZ

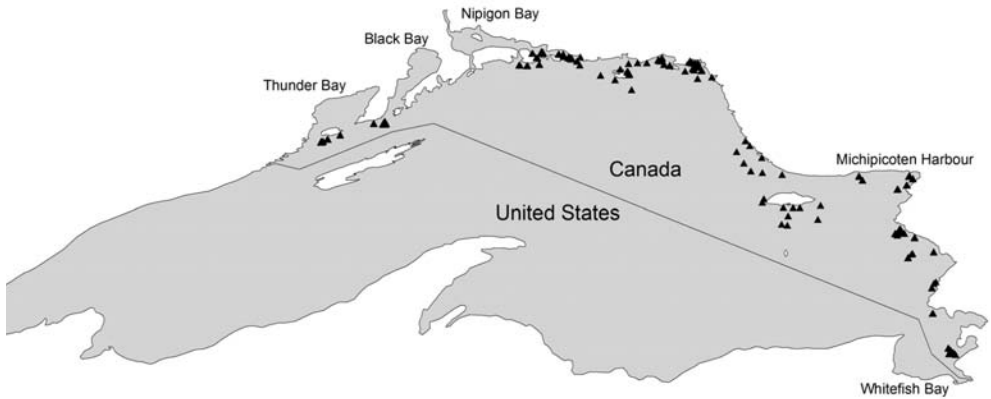


Fig. 1. Map displaying the key sites and net locations from the deepwater cisco survey in Lake Superior.

(1929) used cotton or linen nets instead of nylon. The experimental net consisted of eight randomly assigned 46 m monofilament panels, with stretched mesh sizes of 38, 45, 51, 57, 64, 70, 76, and 89 mm. The experimental nets were designed to capture a wider size range of fishes so that the smaller *C. hoyi* and *C. kiyi* could be better enumerated. Sampling dates and locations, and the number of each net type set in a given year are presented in Table 1. The sampling covered 17 of the Lake Superior fisheries management units. Management units are modified statistical districts previously used for reporting commercial fishery statistics (SMITH et al. 1961; HANSEN et al. 1995).

Gillnets were deployed on the bottom, and minimum and maximum depth data were collected from every net set. Starting in 2007, an Ekman dredge was used to collect a sediment sample from the immediate area where each net gang was set to better understand the habitat preferences of deepwater ciscoes. In addition, a temperature data logger was affixed to each net, and water temperature was recorded at 10 s intervals.

Gillnet catches were tallied on-board by mesh size, and a total weight of fish caught in each net was taken for each species. Ciscoes captured in 2004 and 2006 were tentatively identified to species based on external morphological characteristics (primarily mouth and fin position, gill raker characteristics, and colour) and five individuals from each of the four species were bagged, labelled, and frozen for confirmation of tentative identification, and additional morphometric and biological analyses. Ciscoes were identified with the aid of a variety of unpublished keys. In 2007 and 2008, all ciscoes were frozen and returned to the laboratory for later analyses.

In the laboratory, frozen fish were thawed, photographed (full body, head, and gill rakers), weighed, and total length recorded. Fish were identified by three biologists, and any potential changes in clas-

Table 1. The sampling locations, dates, and number of net sets for each of the four years of deepwater cisco sampling in Lake Superior.

Year	Sampling location	Dates	# experimental nets	# traditional nets
2004	Rosspoint	September 14–23	0	27
2006	Thunder Bay	June 12–21	5	11
	Rosspoint to Marathon	August 9–17	15	21
2007	Sault Ste Marie to Wawa	June 19–July 18	17	10
2008	Wawa to Rosspoint	June 8–July 7	24	10

sification were noted. A number of specimens had characteristics from more than one species; these fish were classified as hybrids with the species for which they most closely fit the criteria listed first (e.g., a shortjaw/bloater would have more shortjaw cisco characteristics than bloater characteristics). In 2006, a chest freezer failed and most of the collected specimens spoiled, and identifications could not be revisited. Gill rakers and a tissue sample for future genetic analysis were removed and stored in 70% ethanol. Aging structures (scales and otoliths) were also collected, and individuals were examined for sex determination and state of maturity for an expected life history examination.

Data analyses

The relative abundance of ciscoes was assessed using the combined mesh size capture data from over-night gillnet sets, except for three nets that were left for two nights due to adverse weather conditions. For those three sets, the catch was divided by two, and those data were used in the analyses. Only nets that were set 60 m or deeper were used in the following analyses. The relative abundance of *C. artedii*, *C. hoyi*, *C. kiyi*, and *C. zenithicus* was compared from the Canadian waters of Lake Superior from three areas: western (fisheries management units 5 and 6), northern (fisheries management units 11, 12, 17, 18, 19, 20, and 21) and eastern (fisheries management units 23, 24, 26, 27, 28, 31, 33, and 34) waters via one-way analyses of variance. Data were $\ln(x+1)$ transformed to meet the assumptions of homogeneity of variance and normality of the residuals. When significant differences were detected, Tukey HSD tests were used to distinguish among areas (ZAR 1999). Bonferroni corrections were applied to ensure that the question-wise probability remained at $\alpha = 0.05$. Only data from experimental gillnets were used in this analysis as the mesh sizes of the traditional nets do not effectively capture *C. hoyi* or *C. kiyi*. The relative abundance data for both the traditional and experimental nets were converted to fish per gillnet kilometre, and the results displayed by fisheries management unit.

Specific locations in Canadian waters initially fished by KOELZ (1929) were targeted during the surveys to allow a contrast in the coregonid community over the past 80 years. Traditional nets fished from all depths were used in this analysis. In addition to the four cisco species, the lake whitefish *C. clupeaformis* was included in this examination. Nets of various lengths were often fished for more than one night in the KOELZ (1929) survey, so the number of fish captured in these sets was adjusted to reflect the relative abundance captured per net kilometre over a single night of effort. Two species identified by KOELZ (1929), *C. reighardi* and *C. nigrippinus*, were later synonymized with *C. zenithicus* and included in the totals for that species (TODD & SMITH 1980, TODD et al. 1981). Differences in the composition of the coregonid community at specific sites surveyed by KOELZ (1929) and the contemporary surveys was assessed using log-linear analysis (ZAR 1999). Bonferroni corrections were applied to ensure that the question-wise probability remained at $\alpha = 0.05$. The use of log-linear analyses was not possible for the Alona Bay, Quebec Harbour, Silver Islet, and Thunder Cape sites because the communities were too simple and there were too many empty cells in the analysis. The total number of coregonids captured at the sites was compared between the KOELZ (1929) and contemporary surveys using a paired t-test to determine if observed changes in community composition reflected losses of coregonids or a potential redistribution of fishes within the community. Data were $\ln(x+1)$ transformed to meet the assumption of homogeneity of variances required for the use of parametric statistics.

A standard multiple regression approach was used to evaluate whether any of four habitat parameters—slope, depth, temperature and substrate type—were able to account for significant variation in the number of each cisco species that was captured at each site. Catch data were $\ln(x+1)$ transformed to meet the assumptions of homogeneity of variance and normality of residuals. The analysis was limited to experimental nets from 2007–2008 because temperature and substrate data were only available from that timeframe, and the traditional nets sampled *C. hoyi* and *C. kiyi* poorly. Slope was calculated as the percent change in depth from the shallowest to deepest part of a net set. Depth was the mean depth of the set, temperature was the mean bottom temperature during the net set, and substrate was classified as the dominant substrate type (sand, silt or clay) from the bottom grab. Rough weather that prevented substrate sampling and a broken temperature logger resulted in a few instances where these data were not available for a given net; after excluding these sites from the analysis, 39 sites remained. To allow

a better understanding of the influence of depth on the distribution of the four cisco species, all experimental net sets ($n = 72$) were divided into 20 m depth bins and the mean catch per depth bin was plotted for each species. Depth data were further divided into 10 m depth bins, and the depths at which more than 50% of the cumulative catch for that species occurred were highlighted as the abundance median as per SELGEBY & HOFF (1996). Similarly, substrate data ($n = 41$ sites) were plotted with mean catch data to further elucidate habitat preferences.

Results

A total of 4249 ciscoes were collected from the 140 net sets. *C. hoyi* and *C. artedi* made up the majority of the cisco catch in both the experimental ($n = 61$) and traditional ($n = 79$) nets (Table 2). The patterns of relative abundance for the four cisco species were similar, with lower abundance generally observed in the eastern basin. The relative abundance of *C. artedi* significantly differed among areas ($F_{2,58} = 7.5$; $P = 0.001$), with fewer individuals found in the eastern waters of Lake Superior than in either the western or northern areas (eastern vs. western Tukey HSD $P = 0.009$; eastern vs. northern Tukey HSD $P = 0.007$; Fig. 2). This pattern is readily apparent in *C. artedi* abundance by management unit from both the experimental and traditional nets. High relative abundance was noted in the management units nearest the shore close to Thunder Bay and along the north shore, but with the exception of a couple of the Michipicoten Harbour and Whitefish Bay management units from the experimental nets, relative abundance along the eastern shore was low (Fig. 3a, b).

Table 2. The total number of ciscoes captured in experimental ($n = 61$) and traditional ($n = 79$) gillnets set in the Canadian waters of Lake Superior.

Net type	<i>C. artedi</i>	<i>C. hoyi</i>	<i>C. kiyi</i>	<i>C. zenithicus</i>
Experimental	542	1294	313	345
Traditional	889	613	51	202

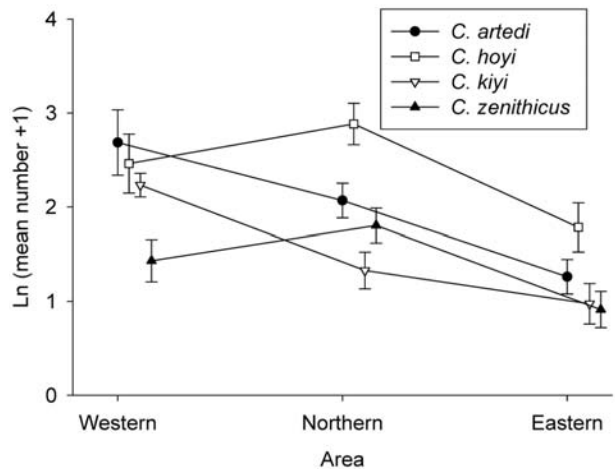


Fig. 2. The relative abundance of *Coregonus artedi*, *C. hoyi*, *C. kiyi*, and *C. zenithicus* collected in experimental gillnets from three broad areas (western, northern, and eastern) in the Canadian waters of Lake Superior.

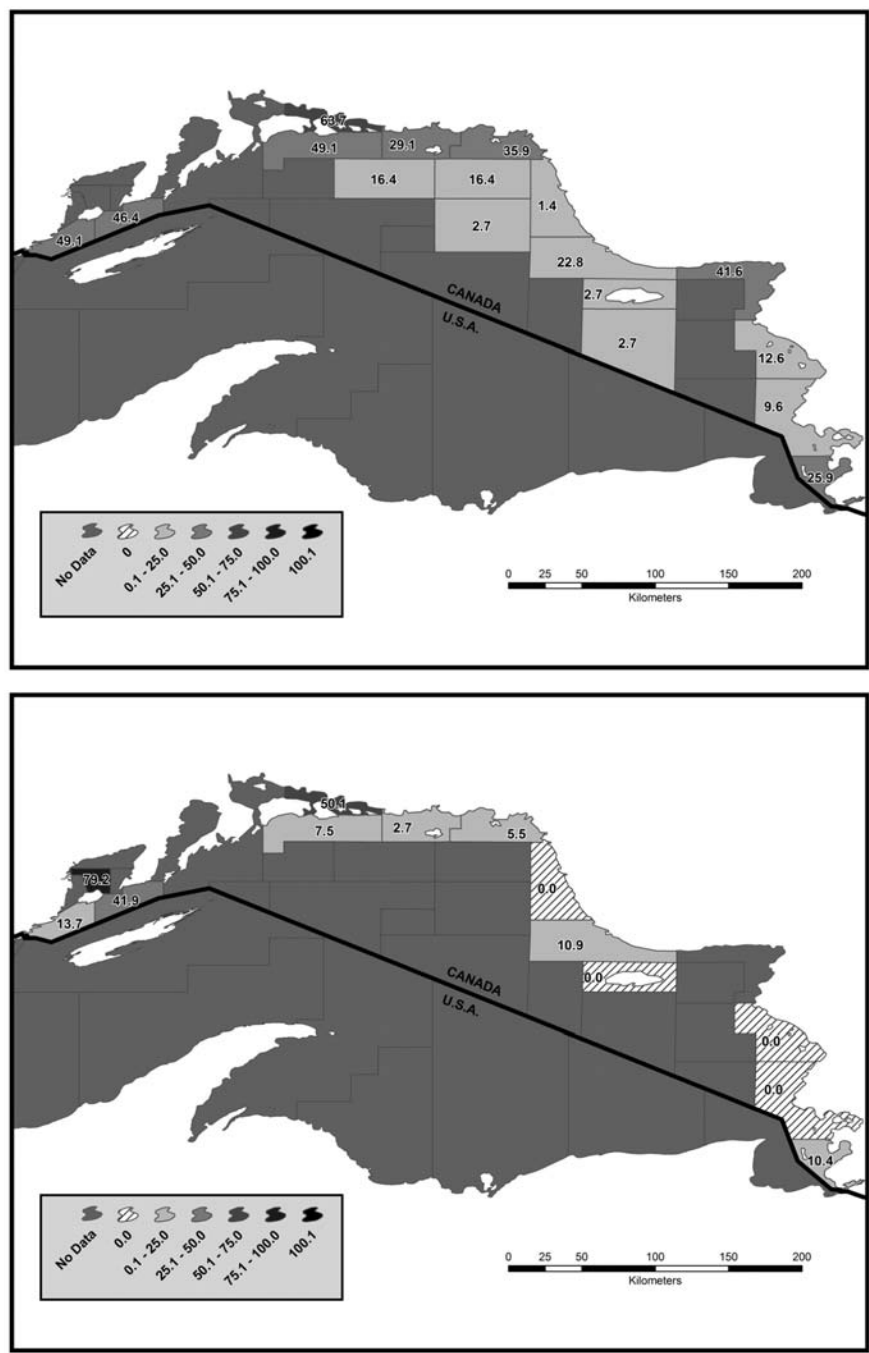


Fig. 3. The mean number of *Coregonus artedii* captured per gillnet km from the Canadian management units of Lake Superior in 2004–2008 using a) experimental and b) traditional gill nets fished at depth 60 m or greater.

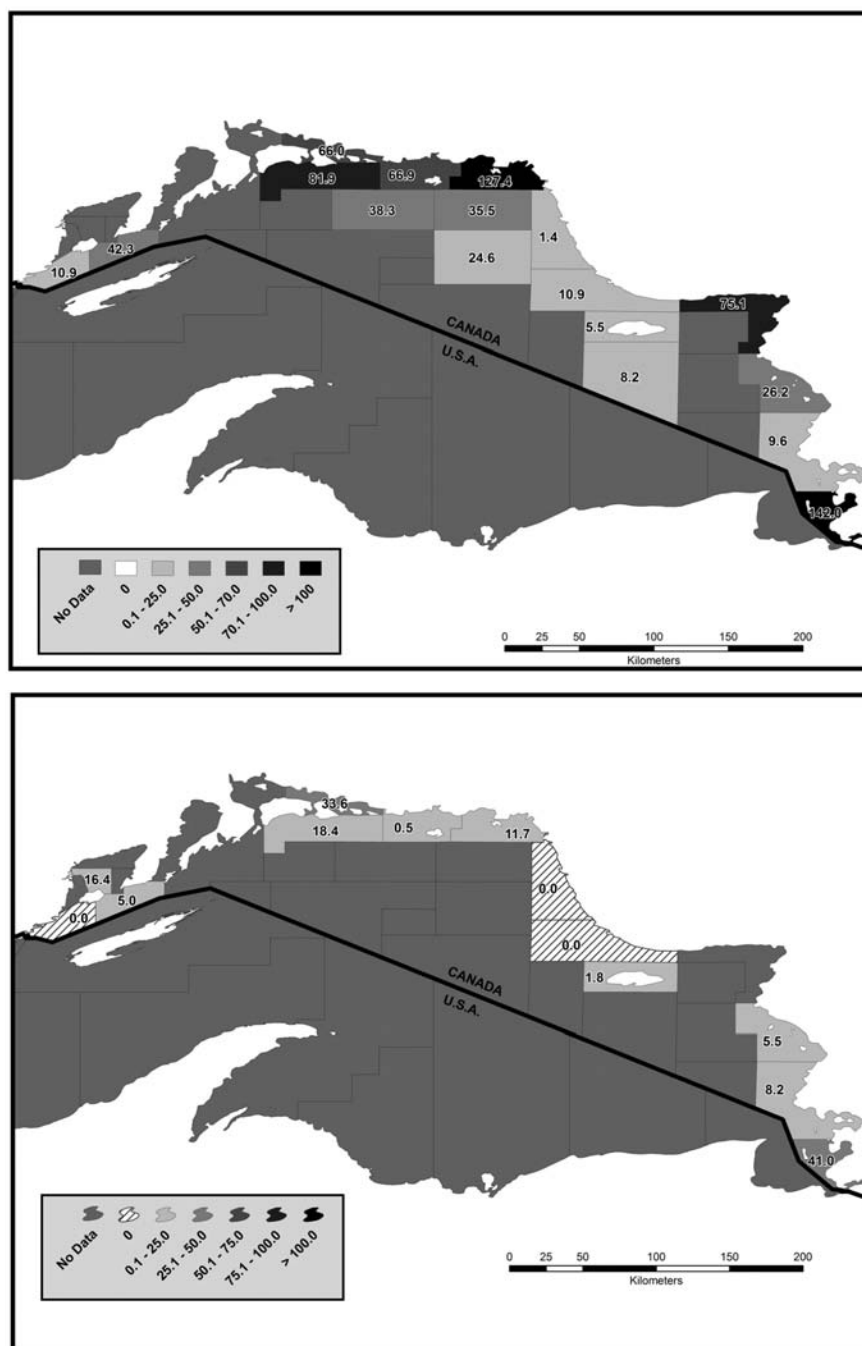
The relative abundance of *C. hoyi* differed among areas ($F_{2,58} = 5.5$; $P = 0.006$, with lower abundance in eastern areas than northern areas (eastern vs. northern Tukey HSD $P = 0.004$; Fig. 2). Traditional nets were ineffective at sampling the relatively small *C. hoyi*, as only the management units near the village of Rossport and in Whitefish Bay had reasonable catches (Fig. 4b). *C. hoyi* was captured in high abundance along the north shore management unit in experimental nets, and there were pockets of high abundance in Whitefish Bay, Michipicoten Harbour and near Black Bay (Fig. 4a).

After applying the Bonferroni correction, no differences in relative abundance were observed in *C. kiyi* from the western, northern and eastern areas of Lake Superior ($F_{2,58} = 3.2$; $P = 0.048$; Fig. 2). Likely because of its small size, *C. kiyi* was not often captured in traditional nets (Fig. 5b), and, with the exception of Michipicoten Harbour *C. kiyi* was almost absent from eastern waters in the experimental nets (Fig. 5a). *C. kiyi* was the most abundant in offshore zones along the north shore, and was detected in moderate abundance in western waters (Fig. 5a).

Patterns of *C. zenithicus* relative abundance were similar to those of *C. hoyi*, with significant differences detected among areas ($F_{2,58} = 5.9$; $P = 0.004$), and lower abundance in eastern areas than northern areas (eastern vs. northern Tukey HSD $P = 0.003$; Fig. 2). Outside of the north shore, only the Michipicoten Harbour management unit had high relative abundance in experimental nets (Fig. 6a), while *C. zenithicus* was consistently captured in low abundance in the majority of management units that were sampled (Fig. 6b).

The historic Lake Superior coregonid community was quite different than the community that exists today. *C. zenithicus* was the dominant coregonid in the KOELZ (1929) surveys, making up more than 90% of the catch. In contrast, *C. artedi* and *C. hoyi* were the dominant ciscoes at most sites today (Table 3). The coregonid community composition has significantly changed in every area of the lake (Table 4), primarily due to the decline in *C. zenithicus*. The total number of coregonids that were captured has not significantly changed over that time period ($t = 1.81$, $df = 9$, $P = 0.11$), although there may be patterns among different areas of the lake. Catches from the majority of sites in eastern and western Lake Superior had declined, while those along the north shore had not (Table 3).

The four habitat attributes (slope, temperature, substrate type and depth) significantly accounted for part of the variation in the capture of the four Lake Superior ciscoes, ranging from 30% of the *C. artedi* capture variation to 72% of the *C. kiyi* capture variation (Table 5). Depth significantly contributed to the multiple regression models for all four species, while substrate significantly contributed to all but the *C. kiyi* model (Table 5). Temperature never significantly added to any model, and slope was only identified as important for *C. hoyi* (Table 5). *C. artedi* was captured at all depths, with a general trend of decreasing abundance with increasing depth (Fig. 7a), and the abundance median was 50–70 m for this species (Fig. 7b). *C. kiyi* displayed the opposite trend, increasing in abundance with increasing depth (Fig. 7a). *C. kiyi* was not captured at depths <70 m, and had the deepest abundance median (Fig. 7b). Both *C. hoyi* and *C. zenithicus* were absent at the shallowest depths, most abundant at intermediate depths and declined in abundance at the deepest depths, although the pattern for *C. zenithicus* was slightly deeper than *C. hoyi* (Fig. 7a, 7b). Sand-dominated substrates were the least utilized for all species, with catches of *C. artedi*, *C. hoyi* and *C. zenithicus* being highest on silt-dominated substrates (Table 5, Fig. 8).



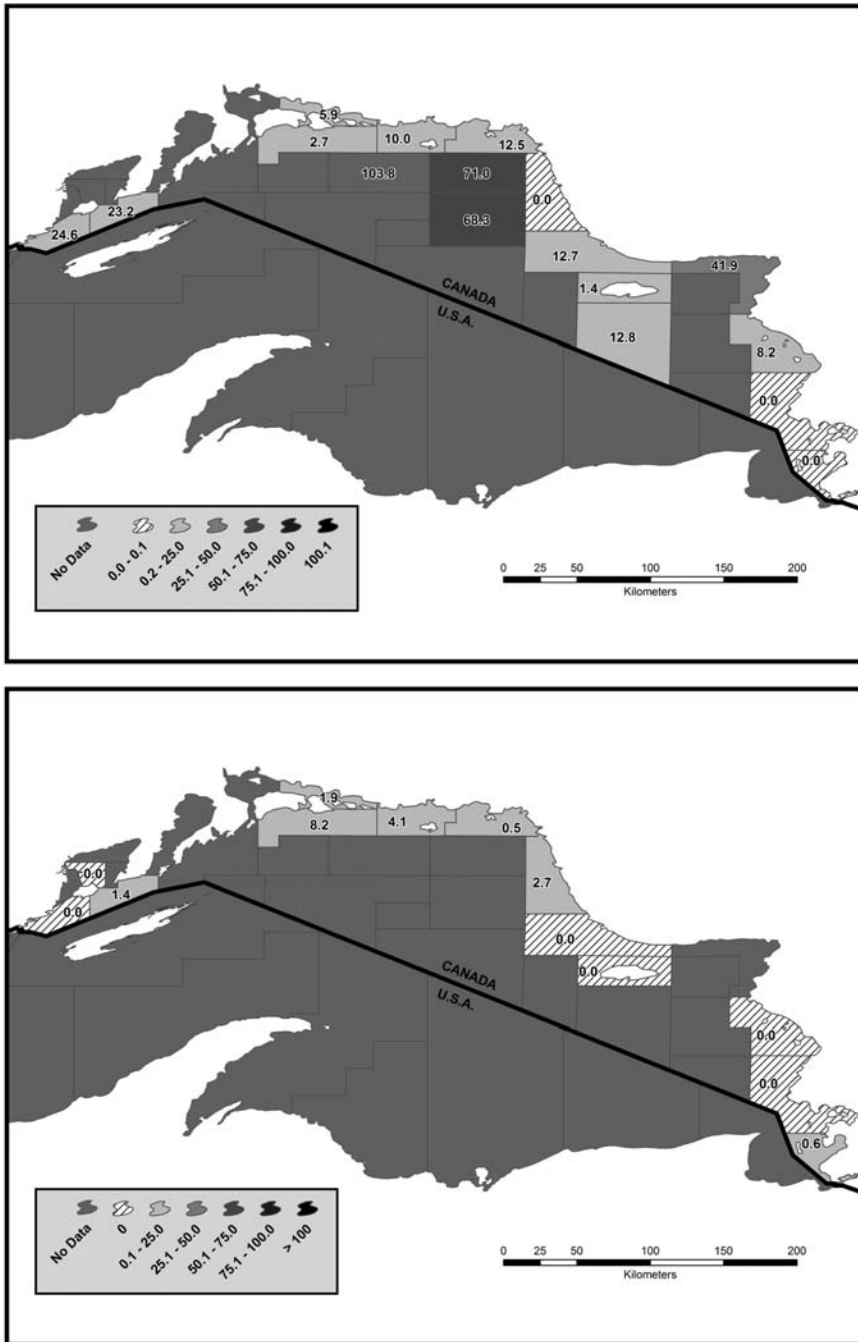


Fig. 5. The mean number of *Coregonus kiyi* captured per gillnet km from the Canadian management units of Lake Superior in 2004–2008 using a) experimental and b) traditional gill nets fished at depth 60 m or greater.

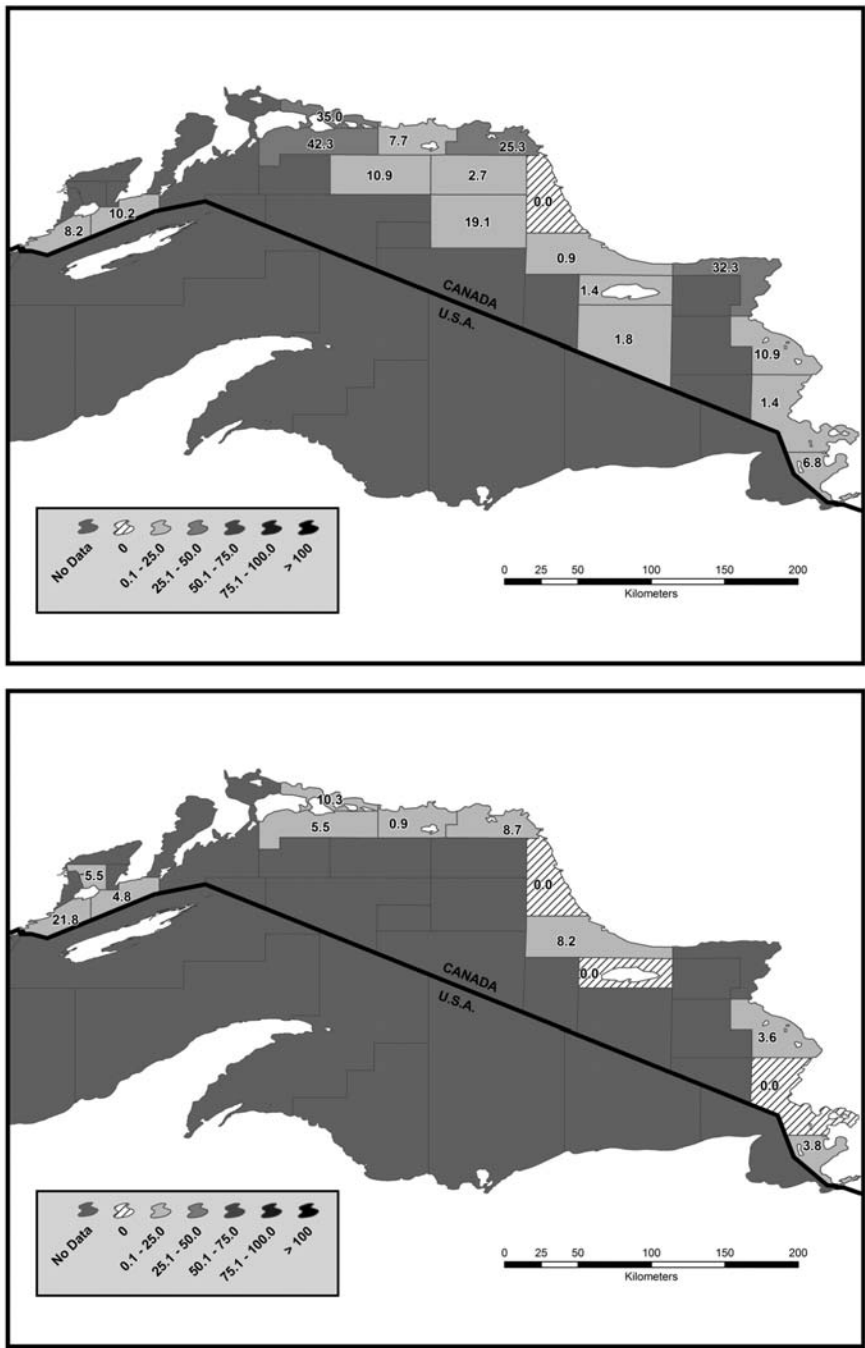


Fig. 6. The mean number of *Coregonus zenithicus* captured per gill net km from the Canadian management units of Lake Superior in 2004-2008 using a) experimental and b) traditional gillnets fished at depth 60 m or greater.

Table 3. A comparison of *Coregonus spp.* captured in the same location by KOELZ (1929) and the contemporary DFO surveys. Numbers in parentheses represent standard errors.

Location	Site	Survey	n	Mean depth (m)	<i>C. artedii</i>	<i>C. clupei-formis</i>	<i>C. hoyi</i>	<i>C. kiyi</i>	<i>C. zenithicus</i>	Total
Sault Ste Marie	Whitefish Bay	Koelz	1	69.5	3.6 (-)	1.8 (-)	0.0 (-)	0.0 (-)	182.3 (-)	187.7 (-)
		DFO	4	71.0	8.9 (4.1)	0.7 (0.7)	47.8 (10.6)	0.0 (0.0)	4.8 (2.3)	62.2 (9.5)
Coppermine Point	Off Alona Bay	Koelz	1	109.7	0.0 (-)	0.0 (-)	0.0 (-)	0.0 (-)	72.9 (-)	72.9 (-)
		DFO	1	110.9	0.0 (-)	0.0 (-)	8.2 (-)	0.0 (-)	0.0 (-)	8.2 (-)
Michipicoten Island	3 miles SE of Quebec Harbour	Koelz	1	146.3	0.0 (-)	0.0 (-)	0.0 (-)	0.0 (-)	32.8 (-)	32.8 (-)
		DFO	1	150.3	0.0 (-)	0.0 (-)	5.5 (-)	0.0 (-)	0.0 (-)	5.5 (-)
Rosspoint	Off Bread Rock	Koelz	1	155.5	3.3 (-)	0.0 (-)	6.6 (-)	0.0 (-)	172.2 (-)	182.1 (-)
		DFO	2	152.9	13.7 (13.7)	0.0 (-)	10.7 (2.7)	0.0 (-)	8.2 (8.2)	32.8 (24.6)
	Simpson Channel	Koelz	1	135.3	0.0 (-)	0.0 (-)	0.0 (-)	0.0 (-)	13.1 (-)	13.1 (-)
		DFO	3	133.2	6.4 (5.1)	13.7 (6.3)	2.7 (2.7)	0.0 (-)	9.1 (5.1)	31.9 (5.6)
	Off Salter Island	Koelz	1	76.8	0.0 (-)	0.0 (-)	6.6 (-)	0.0 (-)	22.1 (-)	28.7 (-)
		DFO	13	78.3	69.2 (13.6)	24.5 (2.7)	54.3 (12.3)	3.8 (2.9)	16.0 (4.8)	167.7 (27.4)
Thunder Bay	Moffat Strait	Koelz	1	24.7	23.0 (-)	26.2 (-)	0.0 (-)	0.0 (-)	16.4 (-)	65.6 (-)
		DFO	1	28.3	16.4 (-)	68.4 (-)	0.0 (-)	0.0 (-)	0.0 (-)	84.8 (-)
	North Silver Islet	Koelz	1	25.6	0.0 (-)	0.0 (-)	0.0 (-)	0.0 (-)	144.4 (-)	144.4 (-)
		DFO	1	18.0	19.1 (-)	0.0 (-)	0.0 (-)	0.0 (-)	0.0 (-)	19.1 (-)
	Off Thunder Cape	Koelz	1	56.7	0.0 (-)	0.0 (-)	0.0 (-)	0.0 (-)	45.9 (-)	45.9 (-)
		DFO	2	51.2	34.2 (17.8)	0.0 (-)	0.0 (-)	0.0 (-)	0.0 (-)	34.2 (17.8)
Welcome Island	South	Koelz	1	42.1	0.0 (-)	0.0 (-)	23.0 (-)	0.0 (-)	193.6 (-)	216.5 (-)
		DFO	2	49.8	37.6 (6.6)	2.1 (1.1)	2.1 (0.7)	0.0 (-)	0.2 (0.2)	41.8 (7.1)

Table 4. Log-linear analysis results of coregonid species composition from sites fished by KOELZ (1929) and revisited by this study.

Location	Site	Maximum likelihood χ^2	Probability
Sault Ste Marie	Whitefish Bay	212.5	<0.001
Rossport	Off Bread Rock	77.4	<0.001
	Simpson Channel	18.3	0.001
	Off Salter Island	62.3	<0.001
	Moffat Strait	37.6	<0.001
	South Welcome Island	203.7	<0.001

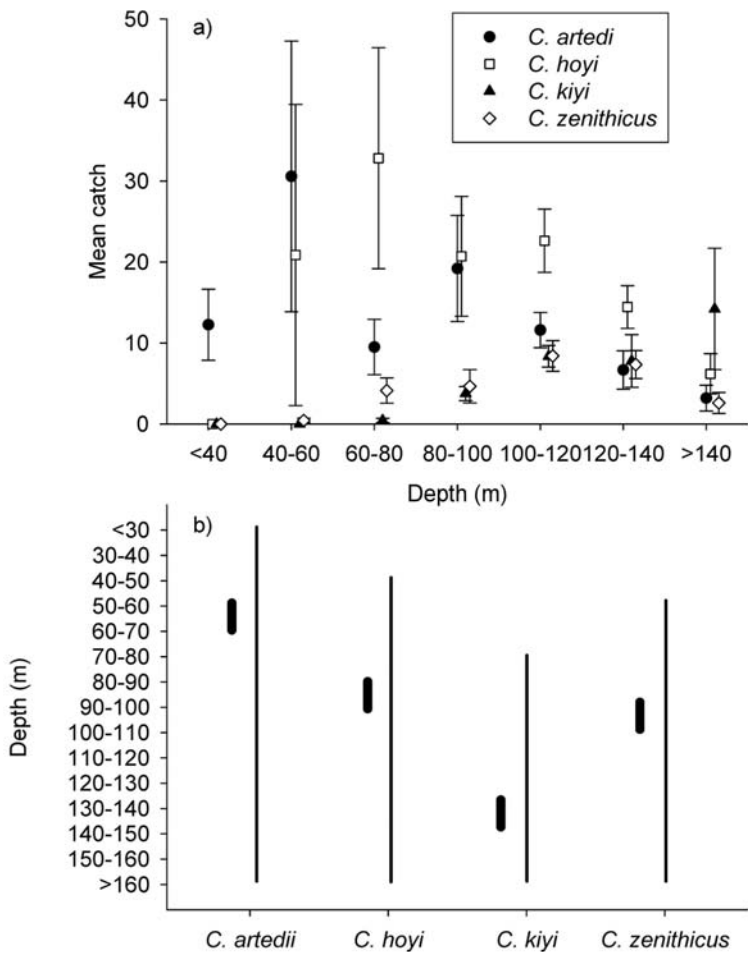


Fig. 7. a) The mean capture of *Coregonus artedii*, *C. hoyi*, *C. kiyi*, *C. zenithicus* from the experimental gillnets by depth bin. Error bars represent standard deviation. b) The range of depths of capture (thin line) and the depth at which more than 50% of the cumulative catch for that species occurred (thick line) for *Coregonus artedii*, *C. hoyi*, *C. kiyi*, and *C. zenithicus*.

Table 5. Multiple regression results and estimates for the intercept (β_0) and predictor variables (β_i 's) used to evaluate habitat variables in the cisco habitat preference models. The predictor variables included slope (SLOPE), temperature (TEMP, in °C), dominant substrate type (SUBS; sand, silt or clay) and depth (DEPTH, in m). Significant predictor variables are marked with an asterisk.

Species	SLOPE		TEMP		SUBS		DEPTH		R^2	F	df	P
	β_0	β_{SLOPE}	β_{TEMP}	P	B_{SUBS}	P	β_{DEPTH}	P				
<i>C. artedi</i>	40.59	0.129	0.380	0.221	0.202	0.049*	0.422	0.009*	0.30	3.64	4,34	0.014
<i>C. hoyi</i>	74.77	0.250	0.044*	0.236	0.088	0.002*	0.531	<0.001*	0.52	9.21	4,34	<0.001
<i>C. kiyi</i>	-2.77	-0.032	0.723	0.197	0.062	0.924	0.888	<0.001*	0.72	22.26	4,34	<0.001
<i>C. zenithicus</i>	34.5	0.133	0.286	0.241	0.088	0.159*	0.633	<0.001*	0.50	8.48	4,34	<0.001

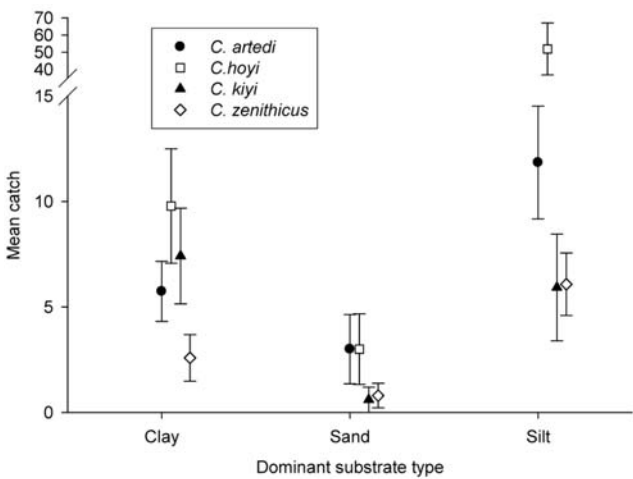


Fig. 8. The mean number of *Coregonus artedi*, *C. hoyi*, *C. kiyi*, and *C. zenithicus* by dominant substrate type caught in experimental gillnets in Lake Superior.

Discussion

Coregonids remain the dominant prey for piscivorous fishes in the Canadian waters of Lake Superior, despite significant changes in the community since the surveys of KOELZ (1929). Overexploitation and the introduction of invasive species decimated the nearshore and offshore fish communities in Lake Superior by the mid-20th century (LAWRIE & RAHRER 1972, BRONTE et al. 2003), and the fish community has been slowly evolving since that time. *C. artedi* populations began recovering in the 1970s and are now considered to be at their former historic abundance levels (EBENER et al. 2009). *C. hoyi* populations exploded in the United States waters of Lake Superior in the mid-1980s (BRONTE et al. 2003), and this species is now the lake’s dominant deep-water cisco form. This research confirms that *C. artedi* and *C. hoyi* now dominate the cisco community in Canadian waters as well. While still widely dispersed in Lake Superior, *C. zenithicus* persists at a much lower abundance than it did during historic surveys. The replacement of *C. zenithicus* has been a gradual process; it constituted over 90% of the KOELZ (1929) surveys, 34% of the cisco community in the late 1950s (E.H. BROWN JR., unpublished data, cited in HOFF & TODD 2004), around 11% of the PECK (1977) sam-

ples from the early 1970s, and only 5% of the community along the south shore of Lake Superior in 1999–2001 (HOFF & TODD 2004). *C. zenithicus* made up a higher proportion of the catch (13%) in this survey, which might be interpreted as evidence for limited recovery in the past decade, or that abundance in the Canadian waters of Lake Superior is higher than those in the United States waters. SMITH (1970) hypothesized that the introduction and population growth of alewife (*Alosa pseudoharengus*) populations resulted in the loss of coregonids from the other Great Lakes, and the inability of alewife to establish in Lake Superior may be why ciscoes have persisted in Lake Superior but not the remaining Great Lakes.

Ciscoes are not evenly distributed around the Canadian waters of Lake Superior. In general, eastern management areas had lower relative abundance for all species than northern and western management areas. These patterns may reflect the nearshore habitat available in those broad areas, the location of spawning areas and the location of current fishing effort. The western management areas contain Black Bay and Thunder Bay, two embayments which contain the largest *C. artedii* fisheries on the lake (EBENER et al. 2009). Embayments are the most productive habitats in Lake Superior (DEVINE et al. 2005), and the locations in the eastern management area that did contain relatively high cisco abundance are embayments, including Whitefish Bay and Michipicoten Harbour. Little is known about the spawning areas for deepwater ciscoes, but almost all the known spawning areas for *C. artedii* are in the western part of the lake (EBENER et al. 2009).

Commercial harvest and subsistence harvest is nearly absent along the north shore of Lake Superior, but a large commercial effort exists in the western management areas and an unknown, but presumably significant, First Nation fishery exists in the eastern management areas (EBENER et al. 2009). It is possible that the combination of limited embayment and spawning habitat, and the First Nation fishery are limiting populations in the eastern part of the lake. Regardless of the reason or reasons, the combination of relatively high abundance, good habitat and limited fishery along the north shore may provide opportunities for preserving the ciscoe species of conservation concern (*C. zenithicus* and *C. kiyi*) in Lake Superior. The recent establishment of the Lake Superior National Marine Conservation Area (PARKS CANADA 2007), which encompasses approximately 10,000 km² of lakebed along the north shore, will bring additional resources and attention to conservation concerns in this area.

While there has been no significant decrease in the numbers of coregonid species captured from the contemporary and KOELZ (1929) surveys, there are reductions in the majority of the KOELZ (1929) locations that were revisited. It is important to note that differences in catchability between the gillnets fished by KOELZ (1929) and those in this study likely resulted in an underestimate of the already high historic catches, which would have further increased these differences. The replica nets used in this study were constructed of nylon, which has approximately three times the capture efficiency of the cotton gillnets used by KOELZ (1929) (MCCOMBIE & FRY 1960, PYCHA 1962).

Depth is an important factor for segregating Lake Superior ciscoes, though there is substantial among-species overlap. *C. artedii* was once considered a shallow water species, but there is increasing evidence, including this study, that they can be abundant at depths >100 m (SELGEBY & HOFF 1996, EBENER et al. 2009). However, *C. artedii* remains the dominant shallow water cisco form in the lake and it is not known whether this species spawns in deep water (EBENER et al. 2009). The presence of *C. artedii* outside of its historical depth

range may indicate movement into a feeding niche vacated with the decline of deepwater ciscoes in the lake; this is the proposed mechanism for the apparent sympatric evolution of ciscoes within the Great Lakes (TURGEON & BERNATCHEZ 2003). The depth distributions of *C. hoyi* and *C. zenithicus* overlapped considerably, with *C. zenithicus* found at only slightly deeper depths than its congener. These depth preferences have not changed in Lake Superior over the past few decades (SELGEBY & HOFF 1996, HOFF & TODD 2004), although once *C. hoyi* was thought to have a shallower distribution (KOELZ 1929). *C. kiyi* inhabited the deepest depths, and its abundance appeared to be increasing up to the limits of the depths sampled in this study, suggesting that it may be even more abundant in depths deeper than 140 m. Similar observations were made by SELGEBY & HOFF (1996). Diet is likely the mechanism for maintaining depth segregation, as adult *C. artedi* in Lake Superior remain primarily zooplanktivorous (LINK et al. 1995, JOHNSON et al. 2004), while the remaining species are mostly benthivores, primarily consuming *Mysis relicta* and *Diporeia hoyi* (KOELZ 1929, ANDERSON & SMITH 1971, HOFF & TODD 2004). *C. kiyi* has been shown to undertake extensive daily vertical migrations following *M. relicta* (HRABIK et al. 2006). Given the contrasting abundance trends over the past century, and the spatial and diet overlap between *C. hoyi* and *C. zenithicus*, it is possible that competition between these congeners is responsible for the observed decline in *C. zenithicus*. In general, the depth distributions of all cisco species were deeper than those observed by KOELZ (1929), but this may be due to gear limitations of the early 20th century surveys more than a shift in depth over the past century (HOFF & TODD 2004).

The second important habitat factor influencing abundance for all ciscoes except *C. kiyi* was dominant substrate type. In general, species were more likely to be captured over silt, then clay and finally sand substrates. This pattern is likely related to prey availability; benthic invertebrates such as *D. hoyi* are more abundant over silt than clay-dominated substrates, and sand contains the lowest densities (SLY & CHRISTIE 1992, LOZANO et al. 2001, NALEPA et al. 2003). This is because finer substrates contain more organic material as food for the benthic invertebrates (MARZOLF 1965, SLY & CHRISTIE 1992, LOZANO et al. 2001). Benthivores such as *C. hoyi* and *C. zenithicus* would be expected to congregate in areas of greatest prey production, which would be the finest substrates. Interestingly, in Lake Ontario, there is a relationship between depth and substrate, with shallower depths containing coarser (more sand-dominated) substrates (LOZANO et al. 2001), and there are correspondingly higher densities of invertebrates such as *M. relicta* in deeper depths (LOZANO et al. 2001, RUDSTAM et al. 2008).

In summary, this research provides the first comprehensive survey of coregonids in the Canadian waters of Lake Superior since the KOELZ (1929) survey in the early 20th century. While there have been significant changes in the community since that time, Lake Superior remains the only Great Lake where coregonids remain the dominant prey fishes. All four Lake Superior ciscoes are widely distributed, with lower overall densities in the eastern part of Lake Superior, but higher relative abundance in embayment areas regardless of their position on the lake. Ciscoes are spatially segregated by depth, with *C. artedi* dominating water <60 m, *C. hoyi* and *C. zenithicus* at intermediate depths (80–110 m), and *C. kiyi* dominant in deeper waters (>120 m). The two species of conservation concern, *C. kiyi* and *C. zenithicus*, were most abundant along the north shore of Lake Superior, and the establishment of a National Marine Conservation Area along the north shore should provide momentum for preserving coregonid diversity at these sites.

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